
NORTH AMERICA'S OLDEST MOSASAURS ARE TELEOSTS

J. D. STEWART¹ AND GORDEN L. BELL, JR.²

ABSTRACT. Several authors have made reference to mosasaur remains from Upper Cretaceous rocks of Cenomanian age in Texas. These have been interpreted as the earliest mosasaur fossils known from North America. We here document that these fossils are not those of mosasaurs but of a teleost species, *Pachyrhizodus leptopsis* Cope, 1874. This species has lately been regarded as a junior synonym of *Pachyrhizodus caninus* Cope, 1872, but is, in fact, highly distinctive. The known range of *P. leptopsis* is thus extended downward from the Santonian into the Cenomanian stage, and the species is now known from Kansas, Texas, and Alabama. The oldest valid records of North American mosasaurs are from the Turonian stage.

INTRODUCTION

Mosasaurs are a family of marine varanoid lepidosaurian diapsid reptiles that achieved a cosmopolitan distribution during the latter part of the Cretaceous Period. The primitive type of tooth attachment in lepidosaurs is pleurodonty. The nature of the tooth attachment of the marginal dentition in mosasaurs is a modified form of subthecodonty (Romer, 1956). The mosasaurs achieved this by extending a shelf of solid bone vertically and medial to the bases of the marginal dentition. The teeth are usually conical, often carinate, and are equipped with an expanded bony root. Most authorities who have addressed the early history of mosasaurs have contended that they first occur in North America in Cenomanian sediments (Martin and Stewart, 1977; Russell, 1967; Thurmond, 1969). This interpretation rests entirely upon two fossils collected from Cenomanian horizons in Texas (Stenzel, 1944; Thurmond, 1969). We have examined both of these specimens, which we identify as the remains of a teleost, *Pachyrhizodus leptopsis* Cope, 1874. The only previously recognized specimen of *P. leptopsis* correctly pertaining to this taxon is the holotype, which now consists of two jaw fragments, including the right mandibular symphysis. A detailed account of the osteology of *P. leptopsis* and its correct taxonomic placement will appear elsewhere. We here intend to justify our earlier claim (Stewart and Bell, 1989) that there are no well-established records of Cenomanian mosasaurs in North America and to validate the specific distinction of *P. leptopsis*.

ABBREVIATIONS

Institutional abbreviations here employed are as follows:

AMNH—American Museum of Natural History, New York, New York

FMNH—Field Museum of Natural History, Chicago, Illinois

KUVP—Natural History Museum of the University of Kansas, Lawrence, Kansas

LACM—Natural History Museum of Los Angeles County, Los Angeles, California

SMUSMP—Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas

TMM—Texas Memorial Museum, University of Texas, Austin, Texas.

DISCUSSION

The teleost genus *Pachyrhizodus* Dixon, 1850, is known from rocks of Cretaceous age in Europe (Forey, 1977; Sorbini, 1976), North America (Stewart, 1900; Applegate, 1970), Australia (Bartholomai, 1969), and New Zealand (Wiffen, 1983). Although Forey (1977) concluded that pachyrhizodontids do not share any of the synapomorphies of the Ichthyodectiformes, Osteoglossomorpha, Elopomorpha, or Clupeomorpha, Maisey (1991) proposed that they are of unknown affinities within the Elopoccephala. Pachyrhizodontids seem to be similar to the Salmoniformes, but there is no compelling evidence for the inclusion of the Pachyrhizodontidae in that order. *Pachyrhizodus* species range from 0.5 to 2 m in length. Each jaw is equipped with a single row of conical teeth attached to the jaw in a pleurodont fashion. As the generic name implies, each tooth has a swollen, bony root.

Depending upon the authors, only two or three species are recognized in North American Cretaceous rocks. Cope (1874) proposed the name *Pachyrhizodus leptopsis* for "portions of right and

1. Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

2. Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota 57701.

Table 1. Comparison of mosasaurs and *Pachyrhizodus leptopsis*.

	Mosasaurs	<i>Pachyrhizodus leptopsis</i>
Mandible		
Anterior 2–4 teeth	essentially same size as others	significantly smaller than others
Lingual ridge below teeth	angular above and below	sloping above and rounded below
Ventral lingual ridge	prominent	only a flange present
Symphysis	divided into upper and lower parts	vertical articular surface
Both jaws		
Groove medial to tooth row	present	absent
Substance between tooth bases	bone of attachment	extension of dense bone of jaw
Medial side of jaw	resorption pits on lingual and posterior side of teeth	faint resorption pits on lingual side of teeth
Lateral view	tooth bases prominent	tooth bases not seen
Lingual view	labial side not visible	labial side visible

left dentary bones, with other portions of the cranium” (Cope, 1874:42). Of these, only two jaw fragments, including the anterior end of the right mandible, can now be located in the collections of the American Museum of Natural History (AMNH 1756). Cope illustrated the right mandible of this specimen (Cope, 1875, pl. LI, fig. 8). It seems that the posterior portion of the mandibular fragment shown in pl. LI, fig. 8b, is now lost. Cope (1874, 1875) indicated that the specimen was found in the Niobrara Chalk Formation of Phillips County, Kansas. A label associated with the specimen indicates that it was collected in 1872 in sec. 2, T6S, R9W, Phillips County, Kansas. The only Cretaceous rocks exposed in that part of Phillips County belong to the Smoky Hill Chalk Member of the Niobrara Chalk Formation. The yellow to orange chalk matrix in depressions on AMNH 1756 accord with this assignment. Outcrops of the Smoky Hill Chalk in the vicinity of section 2 are of Late Santonian age (see Stewart, 1988, pl. 1), specifically the zone of *Clioscaphtes choteauensis* Cobban, 1951.

Salient features that Cope used to distinguish *P. leptopsis* from other species of *Pachyrhizodus* are twofold. First, the mandibular symphysis is not incurved but is obliquely truncate. Also, the teeth have an anterior cutting edge (Cope, 1875:225–226). To this, Hay (1903) added that the tooth bases, and the alveoli where the teeth have been lost, are as long when measured parallel to the jaw as they are across the jaw, and that the alveoli where teeth have been lost are nearly circular. The only figures of the type material published to date (Cope, 1875, pl. LI, figs. 8a–c) accurately portray the shape of the mandibular symphysis and the tooth bases. In other species of *Pachyrhizodus*, there is a pronounced medial inflection of the mandibles at the symphysis, the conical teeth lack carinae, and the tooth bases are longer measured across the jaw than along it. The dentary/angular suture lies just below and behind the posterior end of the tooth row in

P. caninus but is well behind and below the end of the tooth row in *P. leptopsis* [compare the dentary of *P. caninus* figured by Cope (1875, pl. L, fig. 1) with the posterior portion of the dentary of *P. leptopsis* he figured (Cope, 1875, pl. LI, fig. 8b)]. Furthermore, the thickening below the anterior part of the mandibular tooth row in *P. leptopsis* is rounded or U-shaped in cross section (Figs. 1A and B) but rather angular ventrally in *P. caninus* (KUV 66112) and *P. minimus* Stewart, 1899 (LACM 130333, 131945). Differences between mandibles of *P. leptopsis* and other *Pachyrhizodus* species are summarized in Table 1.

There have been very few published references to *Pachyrhizodus leptopsis* since the works of Cope. Stewart (1900, pl. LXX, fig. 1) illustrated a mandible (KUV 151) he identified as *Pachyrhizodus leptopsis*, but the shapes of the tooth bases and alveoli demonstrate that this mandible is of some other species of *Pachyrhizodus*, as indicated by Schultze et al. (1982:36–37). Hay (1903) accepted the validity of *P. leptopsis*. Applegate (1970) listed *P. leptopsis* as a junior synonym of *Pachyrhizodus caninus* Cope, 1872.

Stenzel (1944) published the first account of a Texas Cenomanian mosasaur along with descriptions of decapod crustacean fossils. Included in a collection of fossils from the Eagle Ford Formation, he listed specimen 460-2 of the University of Texas Bureau of Economic Geology as mandibular fragments of *Clidastes* sp., identified by J. T. Gregory (Stenzel, 1944:443). (Because that collection is now in the Texas Memorial Museum, the specimen in question hereafter will be referred to as TMM 460-2.) There are four types of fish remains catalogued under the number 460. TMM 460-1 includes 10 fish vertebrae. One belongs to a selachian, one is of a small ichthyodectiform teleost, one belongs to an unidentified teleost, and seven are from a moderately large pachyrhizodontid. TMM 460-2 consists of 10 jaw fragments, 2 possible ceratohyal

or hyomandibular fragments, and 4 fragments that may pertain to the pectoral girdle. The size and preservation of the pachyrhizodontid vertebrae suggest that they belong to the same individual as TMM 460-2, which we here identify as *Pachyrhizodus leptopsis*.

The mandibular segments of TMM 460-2 agree with all of the diagnostic characters provided by Cope (1874, 1875) and Hay (1903) for *Pachyrhizodus leptopsis*. Of the mandibular symphysis, only the lower part of the right side is preserved, but it shows the same absence of a medial inflection as does that of the holotype (Figs. 1A and B). A segment of the left mandible is broken just ahead of the anterior end of the meckelian groove and just behind the symphysis. However, enough of the lingual surface of that jaw is preserved to demonstrate that the left mandible also lacked any medial inflection. Only one tooth, on the premaxilla, is complete enough to preserve a carina, but that is on its posterior side. This may imply that some tooth crowns of *P. leptopsis* have carinae on both the anterior and posterior sides. Only one tooth of the holotype, that of the last (tenth from the front) position on the mandibular symphyseal fragment, is complete enough to show an anterior carina. Neither the tooth of the holotype nor that of TMM 460-2 preserve both aspects. Most of the tooth bases on TMM 460-2 are as deep across the jaw as they are long. The exceptions are those of the premaxilla and the anterior teeth of the mandible and maxillae. Near the anterior end of the mandible and maxillae, the cross sections of the tooth bases have a long axis oriented in an anterolateral-posteromedial plane. At the anterior ends of these bones, the longest axes of the cross sections of the tooth bases are nearly perpendicular to the tooth row. These observations also apply to the mandible of the holotype. TMM 460-2 also includes a fragment of the right mandible containing the last seven teeth and the alveoli. The tooth bases of these are longer parallel to the tooth row than they are wide. This is also true of the other fragment of the holotype. The empty alveoli are nearly circular, as Cope (1874, 1875) observed in the holotype.

A segment of the right mandible of TMM 460-2 preserves the last seven teeth and a considerable area of dentary beneath and behind. On the preserved segment, there is no sign of the dentary/angular suture. The thickening below the anterior part of the mandibular tooth row in TMM 460-2 is well rounded (Fig. 1A).

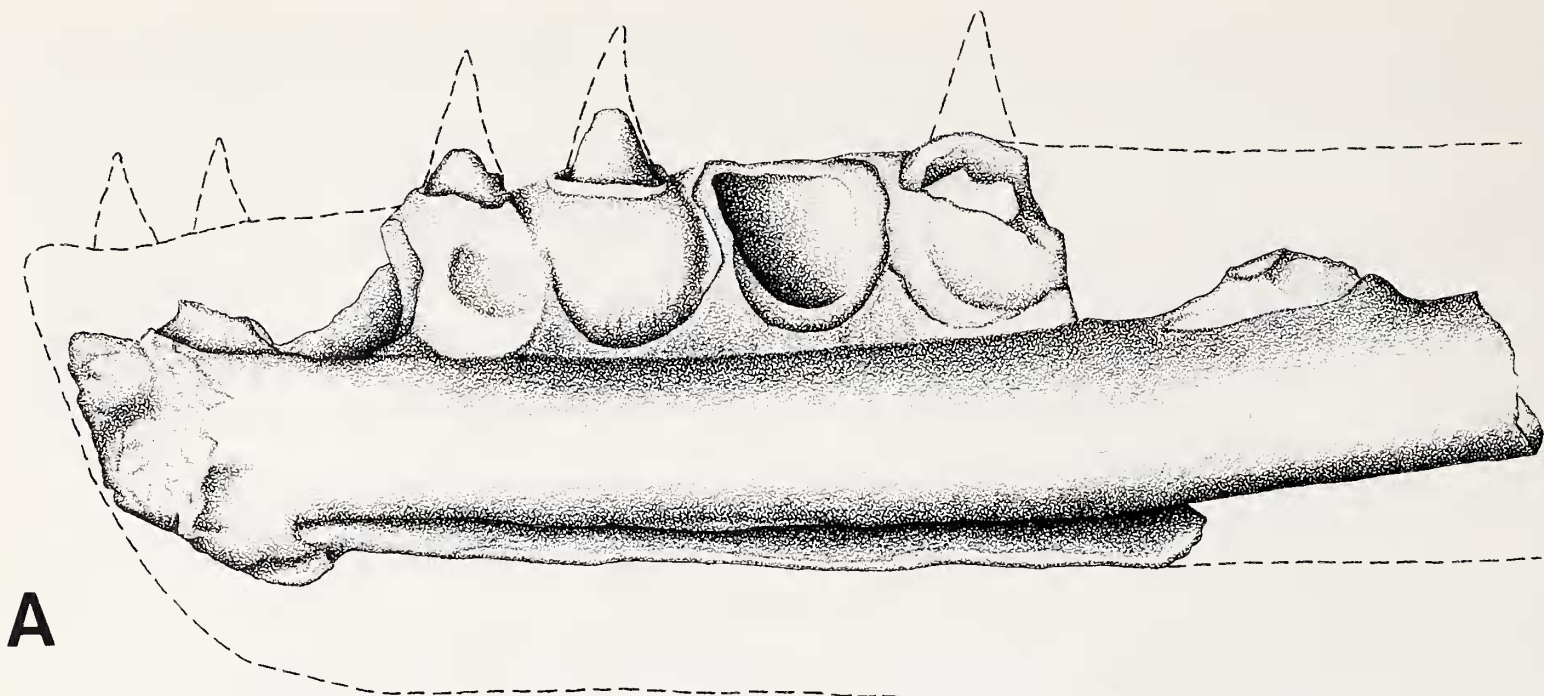
The anterior mandibular portions of TMM 460-2 are nearly twice as large as those of the holotype (Figs. 1 and 2). This indicates that *Pachyrhizodus leptopsis* may have attained lengths as great as the largest *P. caninus*, which is also the largest currently recognized species of the genus in North America. The ventral flange seen in the holotype is not preserved on either mandible of TMM 460-2. Mandibles of *P. caninus* and *P. minimus* have a similar ventral flange.

Except for being larger, the posterior segment of the right mandible of TMM 460-2 accords well with that missing section of the holotype figured by Cope (1875, pl. LI, fig. 8b). It is surprising that even the placement of breaks along the margins of the two specimens is similar. The two mandibular fragments of the holotype and those of TMM 460-2 clearly indicate a thickening of the bone below the anterior part of the tooth row and a deep groove below the thickening. Both the thickening and the groove become subdued posteriorly, resulting in a nearly flat, but slightly convex, surface behind the posterior terminus of the tooth row.

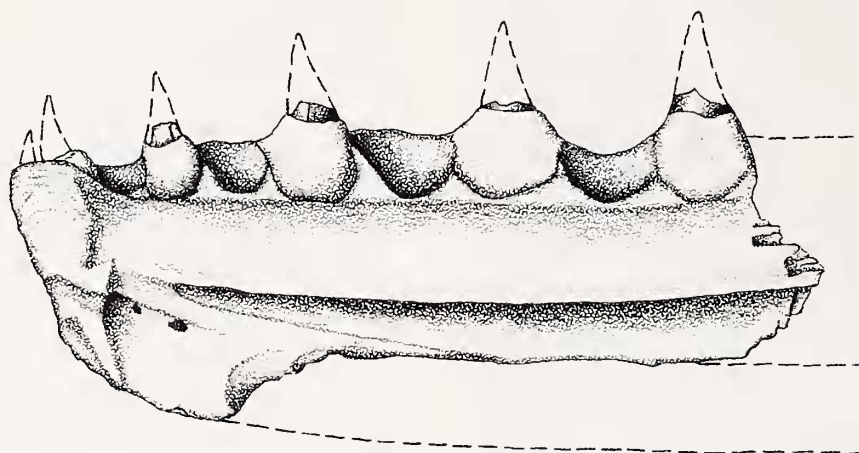
Figures 2A and B illustrate the labial surfaces of the anterior segments of the right mandibles of the holotype of *P. leptopsis* and TMM 460-2. The posterior side of the posterior portion of the right mandible of TMM 460-2 is nearly flat except for compressional distortion. None of the ventral margin is preserved. The equivalent segment of the holotype does preserve a bit of the ventral margin. Only the tops of the bases of the teeth are visible in labial views of TMM 460-2 and the holotype.

One jaw segment of TMM 460-2 is a right premaxilla. The posterior margin is incomplete. As in some salmonids, *Notelops* Woodward, 1901 (Forey, 1977, fig. 4), *Rhacolepis* Agassiz, 1841 (Forey, 1977, fig. 17), and *Pachyrhizodus*, there is an enlarged tooth lingual to the normal row along the labial margin. Only a part of the base of this tooth is present. The inner tooth base is situated against the anteromedial premaxillary margin and the base of the first two labial teeth. Only two teeth and an empty alveolus are preserved in the labial row. As already indicated, enough of the anteriormost tooth is preserved to show that it had a posterior carina. The nature of the anterior side of the tooth is unknown. It is not widely recognized that there are two premaxilla morphologies in large North American *Pachyrhizodus* species in addition to that of *P. leptopsis*. In a specimen identified as *P. caninus* by Stewart (1900, pl. LXX, fig. 3), the inner premaxillary tooth lies against the medial premaxillary margin, but it lies a short distance medial to the labial tooth row and somewhat farther from the anterior margin. Stewart (1900, pl. LXVIII, fig. 2) illustrated a second *Pachyrhizodus* premaxilla morphology, which he tentatively identified as belonging to *P. latimentum* Cope, 1872. In this specimen, the inner tooth row lies on the medial margin of the premaxilla and a small distance from the labial tooth row, but far from the anterior premaxillary extremity. At the widest point of the premaxilla of TMM 460-2, immediately adjacent to the base of the inner tooth, there is a semi-circular rugosity.

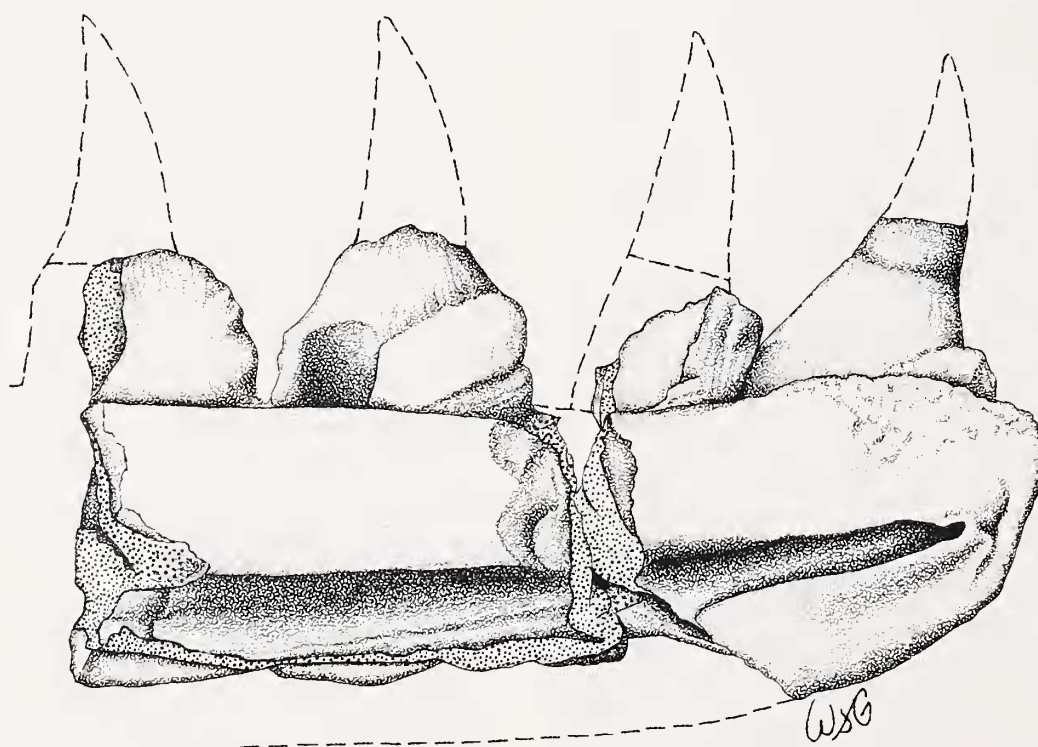
Among the jaw fragments of TMM 460-2 are anterior segments from both maxillae. Both indicate that there is a diminution of the depth of the maxilla four or five tooth positions before the anterior terminus of the tooth row. A flange projects about 18 mm beyond the tooth row of the left



A



B



C

2 cm

maxilla; it is missing in the right. This flange is proportionately longer in *Pachyrhizodus minimus* than in *P. leptopsis*. The dorsal surface of the flange descends gradually ahead of the constriction, and there is a strong longitudinal groove descending anteriorly on the dorso-labial aspect of the flange. This groove is not seen in *P. minimus* or *P. caninus*. The mandible's dorsal surface behind the flange is fairly flat. The flange is thicker on the lingual side than on the labial. The flange bears a complex process not seen on this flange in *P. caninus* and *P. minimus*. This process consists of a ball-like knob directed dorsally. The palatine process of the maxilla of *Elops* Linnaeus, 1766, has a similar appearance (Forey, 1973). In clupeomorphs, there are two such knobs; one is the palatine process, and the anterior one articulates with the mesethmoid. These same two processes exist in ichthyodectiforms, although they are rather flattened. The anterior process (facet for the mesethmoid) is probably the homologue of the ball-like knob in *P. leptopsis*. Ahead of this knob, the flange terminates in a deeply cupped projection. The concavity is directed anteriorly. A similar cupped projection is present in the maxilla of *P. minimus* (LACM 130333, 131945). A broken area in the middle of the dorsal surface behind the knob suggests that another process situated there has been broken off. The labial side of the maxilla is rather smooth and flat, but the medial side is not. There is a strong thickening along the lingual face above the tooth row. Thus, as in the extant salmonids, the labial side of the maxilla is not seen in occlusal (ventral) view, but the lingual side is prominent. This labial thickening continues ahead of the tooth row as the labial side of the anterior flange. Both maxillae show a slight conical projection with a depressed center on the dorso-lingual margin above the fourth tooth from the anterior end. This is probably the facet for the articulation with the palatine. Along the ventral edge of the thickening and a little behind and below that prominence is an elliptical fossa. This fossa is possibly the attachment site for the ligament extending to the palatine. A similar boss and fossa are to be found in a similar position on the maxillae of extant salmonids and esocids. As in the mandible, the tooth bases are clearly seen in lingual view, but not in labial. Most of the tooth bases are circular, although a few are somewhat narrower along the jaw than across it.

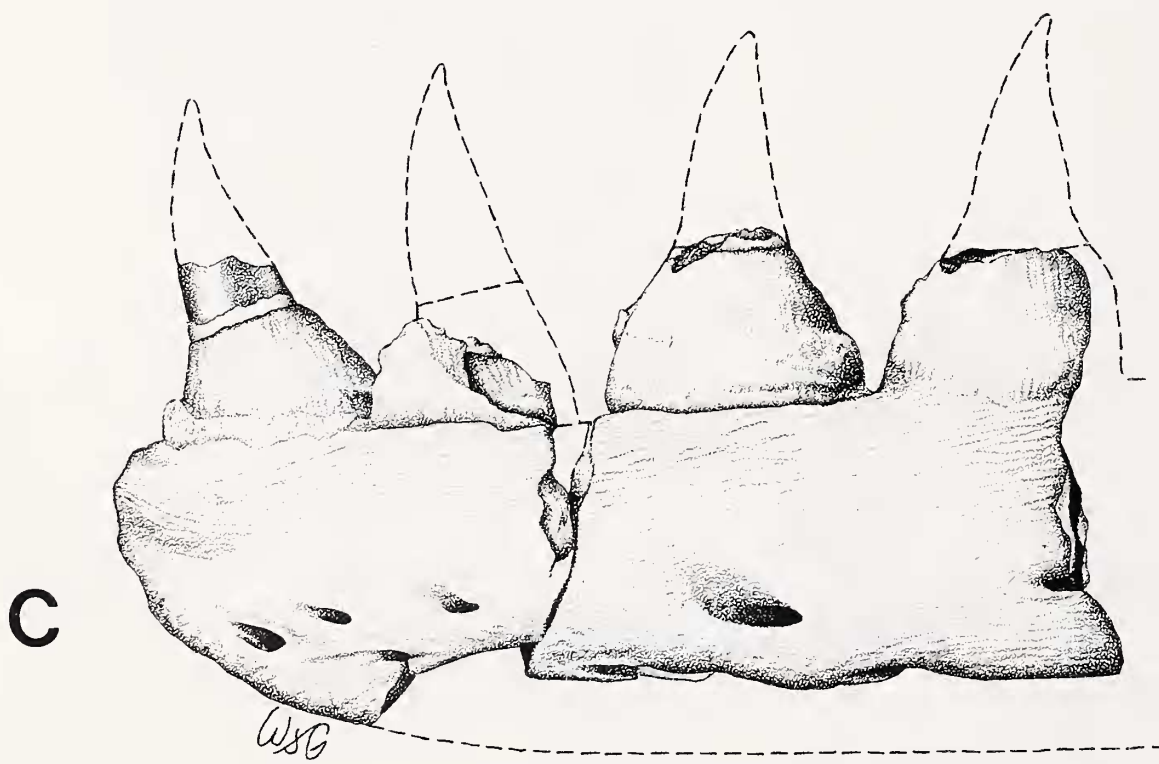
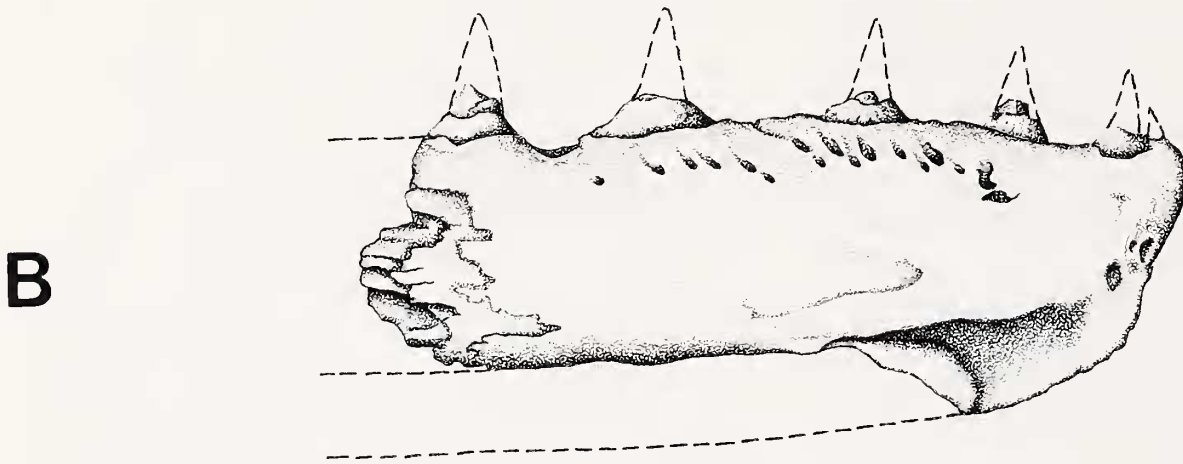
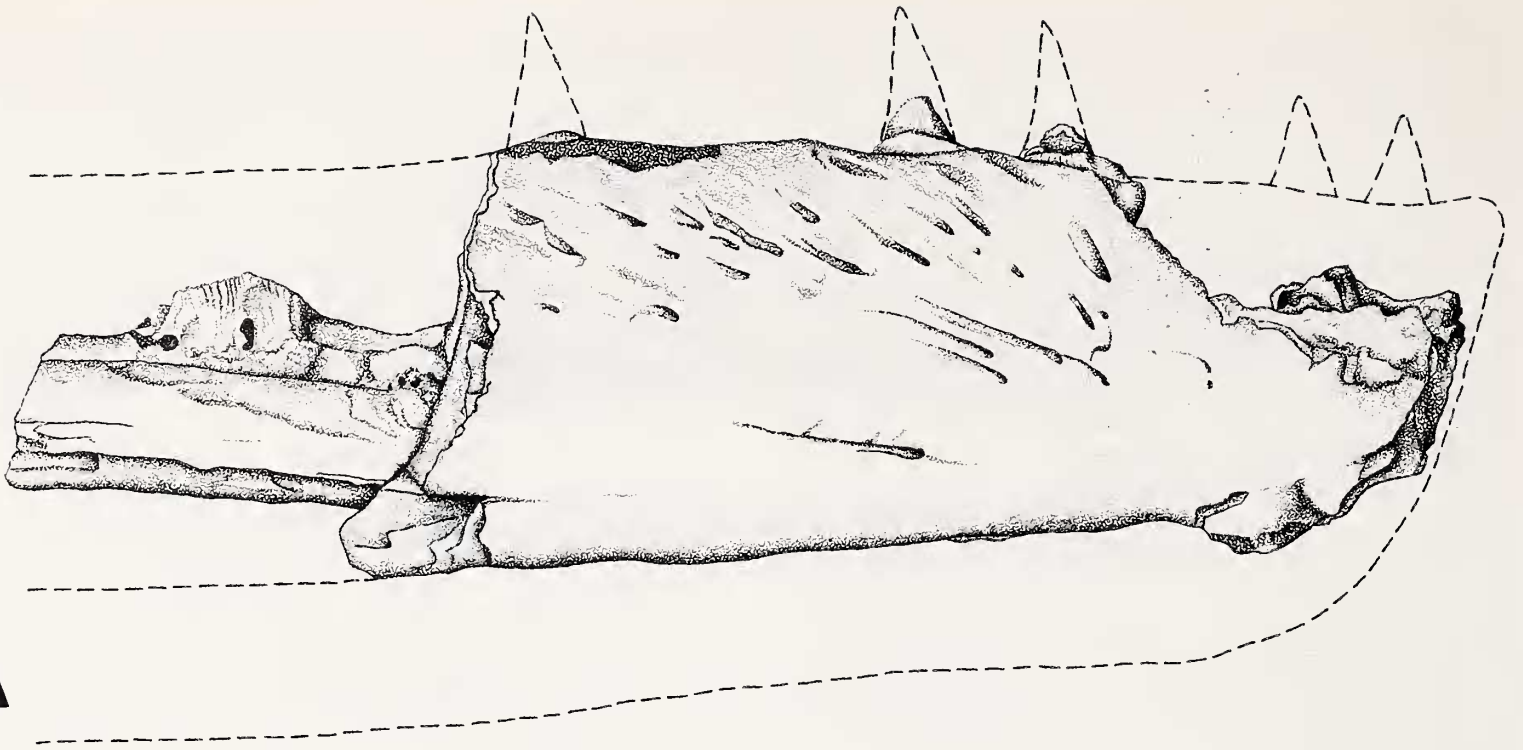
Seven amphicoelous abdominal vertebrae (catalogued with other vertebrae under TMM 460-1) ranging from 31 to 36 mm wide apparently belong to the same individual as the *Pachyrhizodus leptopsis* jaws. Each has a pair of nearly circular depressions for attachment of an autogenous neural arch on its dorsal margin. The anterior and pos-

terior faces have distinct concentric ridges as well as distinct ridges radiating from the center. The first centrum is easily identified by its relative thinness. The thickness of the first centrum is one-third of its maximum depth, which is nearly equal to its maximum width; pits for the neural arch produce a slight depression along the dorsal margin of the centrum in anterior and posterior views. The other six vertebrae are somewhat thicker, the thickness being contained in the height an average of 2.04 times. The faces of the other six centra are roughly oval. The maximum depth averages 91% of the maximum width. The lateral sides of the vertebrae have ornamentation typical of other species of *Pachyrhizodus*. On each side are three to five pits separated by linear ridges. Each ventro-lateral corner of these six centra bears a recess, presumably for a parapophysis. Autogenous parapophyses are found on the first 25 vertebrae of *Rhacolepis buccalis* and the second through the twenty-fifth vertebrae in *Notelops brama*.

No explanation is required to show that the vertebrae do not belong to a mosasaur. It is only the dental remains that tend to be confused with those of mosasaurs. Table 2 summarizes ways in which the dental remains differ. There are at least six features by which mandibles of *Pachyrhizodus leptopsis* may be distinguished from those of mosasaurs in lingual view (compare Figs. 1A and B with C). First, the lingual wall of the jaw covers less of the tooth bases than the labial wall in *P. leptopsis*, but in mosasaurs the sides of the jaw are of nearly the same height. Second, tooth replacement pits lie on the medial side of the tooth base in *P. leptopsis* but on the posteromedial side of the tooth base in mosasaurs. Third, the dense bone of the mandible projects upward between alveoli or tooth bases in *P. leptopsis*. In mosasaurs, the space between tooth bases is occupied by the porous bone composing the tooth bases. Fourth, there is no shelf or groove along the lingual side of the tooth row in *P. leptopsis*, but there is in mosasaurs. Fifth, the mandibular symphysis is not split by the meckelian groove in *P. leptopsis*, but it is in mosasaurs. Sixth, the ventral margin of the mandible in *Pachyrhizodus* is a thin flange. In mosasaurs, the mandibular unit has a robust rounded margin. In addition, the bone texture is laminar in *P. leptopsis* but has a more dense and woven texture in mosasaurs.

The labial view of the mandible furnishes at least two means of distinguishing *Pachyrhizodus leptopsis* mandibles from those of mosasaurs. Most obvious of these is the fact that the tooth bases of *P. leptopsis* are only barely visible (Figs. 2A and B), whereas those of mosasaurs are quite obvious and unobscured (Fig. 2C). Second, there are many small

←
Figure 1. *Pachyrhizodus leptopsis* and mosasaur mandibles in lingual view: **A**, *Pachyrhizodus leptopsis* Cope, 1874, TMM 460-2, right mandible; **B**, *Pachyrhizodus leptopsis* Cope, 1874, holotype, AMNH 1756, right mandible; **C**, *Platecarpus ictericus* (Cope, 1871) LACM 131156 from LACM locality 5597, left mandible.



2cm

	Other <i>Pachyrhizodus</i>	<i>Pachyrhizodus leptopsis</i>
Teeth		
Tooth crowns	conical without carinae	conical with carinae
Tooth bases and alveoli	antero-posteriorly compressed	circular or longer than deep
Mandible		
Tooth row	curves down anteriorly	horizontal anteriorly
Tooth shelf at rear	no thicker than mandible below	significantly thicker than mandible below
Lingual dentary/angular suture	close behind last tooth	behind but remote from last tooth
Symphysis	prominent medial inflection; round symphyseal surface	not medially inflected; vertically elongate symphyseal surface

The teeth possess short stout fangs, occupying alveoli, of which the inner side and part of the anterior and

posterior walls are incomplete. The teeth are, in fact, more or less pleurondont, but the extremity of the root is received into the conic fundus of the alveolus. They bear a superficial resemblance to those of a mosasauroid genus.

We have also seen *Pachyrhizodus leptopsis* jaws catalogued as mosasaurs in other collections. Conversely, Applegate (1970) assigned several mosasaur jaw fragments to *P. caninus* (FMNH P27410, P27516, P27519). Woodward (1905) admitted to having identified a mosasaur jaw as *Pachyrhizodus*. These mistakes are understandable for fragmentary material, but the complete jaws of mosasaurids and pachyrhizodontids have quite different morphologies.

The oldest verifiable published records of North American mosasaurs are of middle to late Turonian age (Martin and Stewart, 1977). There are two unverified published references to possibly pre-Coniacian mosasaurs in Texas. Hill (1901:328) and Adkins (1923:434) listed *Clidastes* Cope, 1868, among other vertebrate genera found at the Eagle Ford–Austin contact southwest of Waco, Texas. These fossils could be of late Turonian to early Coniacian age. There is no indication which elements were the basis for this identification, and the subsequent disposition of the material is uncertain. If the material upon which this identification was based was ever in the Vertebrate Paleontology Laboratory of Texas Memorial Museum, it is no longer there. Adkins (1923) identified a skull of *Mosasaurus* Conybeare, 1822, from near the contact of the Eagle Ford Group and the Austin Chalk. That specimen could have been of a similar age, but it was sent to Sweden. We cannot judge the authenticity of this identification, but no other *Mosasaurus* specimens have been verified from any sediments this old. The only possibly valid record of a Cenomanian mosasaur is based on two unfigured vertebrae from the English Chalk zone of *Holaster subglobosus* (Woodward, 1905).

We conclude this discussion with some observations concerning morphologic stasis in North American teleostean species. *Pachyrhizodus leptopsis* appears to be morphologically static from at least late Cenomanian through Santonian times. With the possible exception of a slight size increase through time, *Xiphactinus audax* Leidy, 1870, *P. minimus* and *P. caninus* seem to be morphologically stable from Turonian through Campanian times (Stewart, in press). *Apsopelix anglicus* (Dixon, 1850) (Teller-Marshall and Bardack, 1978) and *Hoplopteryx lewesiensis* (Mantell, 1822) (Bardack and Teller-Marshall, 1982) show morphological stability throughout much of the Upper Cretaceous not only in North America but in England, as well.

CONCLUSIONS

A specimen previously identified as a mosasaur, TMM 460-1 and 460-2, provides new information on the osteology of *Pachyrhizodus leptopsis*. A

second specimen, SMUSMP 61866, previously identified as a Cenomanian mosasaur from Texas, also proves to be a jaw segment of *Pachyrhizodus*. Cope (1874, 1875) and Hay (1903) were correct to maintain that *P. leptopsis* is morphologically distinct from *P. caninus*. This species also differs from *P. minimus*. *Pachyrhizodus leptopsis* joins a list of other Late Cretaceous teleosts that show no detectable morphological change through three or more stages. With reidentification of these specimens, the oldest North American mosasaur records are of Turonian age.

ACKNOWLEDGMENTS

We offer our sincere thanks to the following individuals for access to specimens in their care: L. Jacobs (SMUSMP), E. L. Lundelius (TMM), J. G. Maisey (AMNH), and H.-P. Schultze (KUV). S. Conkling shared his notes and photographs of some of the Texas fossils. Helpful comments and suggestions were offered by J. M. Harris and L. G. Barnes. All of the illustrations were prepared by Wendy Smith-Griswold, former scientific illustrator of the Earth Sciences Division, LACM.

LITERATURE CITED

- Adkins, W.S. 1923. Geology and mineral resources of McLennan County. *University of Texas Bulletin*, 2340, 202 pp.
- Applegate, S.P. 1970. The vertebrate fauna of the Selma Formation of Alabama, part VII, the fishes. *Fieldiana: Geology Memoirs* 3(8):381–433.
- Bardack, D., and S. Teller-Marshall. 1982. First Cretaceous specimens of the beryciform fish *Hoplopteryx* from North America and their bearing on acanthopterygian evolution. *The Pearce-Sellards Series* 34:1–14.
- Bartholomai, A. 1969. The Lower Cretaceous elopoid fish *Pachyrhizodus marathonensis* (Etheridge Jr). In *Stratigraphy and paleontology; essays in honour of Dorothy Hill*, 249–263. Canberra: Australian National University Press.
- Cope, E.D. 1874. Review of the Vertebrata of the Cretaceous Period found west of the Mississippi River. *Bulletin of the United States Geological and Geographical Survey of the Territories* 2:1–48.
- . 1875. The vertebrata of the Cretaceous formations of the west. *Report of the U.S. Geological Survey of the Territories* 2:1–303.
- Forey, P.L. 1973. A revision of the elopiform fishes, fossil and Recent. *Bulletin of the British Museum (Natural History)*, Geology, Supplement 10, 222 pp.
- . 1977. The osteology of *Notelops* Woodward, *Rhacolepis* Agassiz and *Pachyrhizodus* Dixon (Pisces: Teleostei). *Bulletin of the British Museum (Natural History)*, Geology 28(2):1–204.
- Hay, O.P. 1903. On certain genera and species of North American Cretaceous actinopterosus fishes. *Bulletin of the American Museum of Natural History* 91(95): 1–95.
- Hill, R.T. 1901. Geography and geology of the Black and Grand Prairies, Texas. *U.S. Geological Survey Annual Report* 21(7):1–666.
- Maisey, J.G. 1991. *Rhacolepis* Agassiz, 1841. In *Santana Fossils*, ed. J.G. Maisey, 248–257. Neptune City, New Jersey: T.F.H. Publications.
- Martin, L.D., and J.D. Stewart. 1977. The oldest (Tu-

- ronian) mosasaurs from Kansas. *Journal of Paleontology* 51(5):973–975.
- Romer, A.S. 1956. *Osteology of the Reptiles*. Chicago: The University of Chicago Press, 772 pp.
- Russell, D.A. 1967. Systematics and morphology of American mosasaurs. *Peabody Museum of Natural History, Yale University Bulletin*, 23, 240 pp.
- Schultze, H.-P., J.D. Stewart, A.M. Neuner, and R.W. Coldiron. 1982. Type and figured specimens of fossil vertebrates in the collection of the University of Kansas Museum of Natural History. Part I. Fossil fishes. *University of Kansas Museum of Natural History Miscellaneous Publication*, 73.
- Sorbini, L. 1976. L'itiofauna Cretacea di Cinto Euganeo (Padova-Nord Italia). *Bolletino del Museum Civico di Storia Naturale, Verona* 3:479–567.
- Stenzel, H.B. 1944. Decapod crustaceans from the Cretaceous of Texas. *University of Texas Bulletin* 4401: 401–476.
- Stewart, A. 1900. Teleosts of the Upper Cretaceous. *The University Geological Survey of Kansas* 6(2): 257–380, 383–403.
- Stewart, J.D. 1988. The stratigraphic distribution of late Cretaceous *Protosphyraena* in Kansas and Alabama. *Fort Hays Studies*, 3rd series, science series, no. 10, 80–94.
- . In press. Niobrara Formation vertebrate stratigraphy. *Kansas Geological Survey Guidebook Series*.
- Stewart, J.D., and G. Bell. 1989. The earliest reputed North American mosasaur records are not mosasaurs. *Journal of Vertebrate Paleontology* 9:39A.
- Teller-Marshall, S., and D. Bardack. 1978. The morphology and relationships of the Cretaceous teleost *Apsopelix*. *Fieldiana: Geology* 41:1–35.
- Thurmond, J.T. 1969. Notes on mosasaurs from Texas. *Texas Journal of Science* 21:69–80.
- Wiffen, J. 1983. The first record of *Pachyrhizodus caninus* Cope (Order Clupeiformes) from the Late Cretaceous of New Zealand. *New Zealand Journal of Geology and Geophysics* 26:109–119.
- Woodward, A.S. 1905. Note on some portions of mosasaurian jaws obtained by Mr. G. E. Dibley from the Middle Chalk of Cuxton, Kent. *Proceedings of the Geological Association* 19:185–187.

Received 28 July 1992; accepted 16 November 1993.